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Population Genetic Analysis of a Bread Wheat Panel from Northern and Huang-Huai Agro-Ecological Regions in China

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Abstract: Bread wheat (*Triticum aestivum* L.) is one of the most extensively cultivated cereal crops around the world. Here, we investigated the population structure and genetic diversity of a panel mainly originated from two wheat agro-ecological regions (northern winter wheat region, NW; and the Huang-Huai River Valley's facultative wheat region, HH) in China based on a 15K SNP array. Population genetic analysis revealed that the optimal population number (K) was three, and the three groups were roughly related to ecological regions, including NW (mainly Hebei), HH1 (Henan-Shaanxi), and HH2 (Shandong). Within HH, HH1 had a higher nucleotide diversity (π = 0.31167), minor allele frequency (MAF = 0.2663), polymorphism information content (PIC = 0.2668), and expected heterozygosity (H_{exp} = 0.3346) than HH2. Furthermore, our results demonstrated that genetic diversity decreases with the advancement of wheat breeding. Finally, inference of ancestry informative markers indicated that the genomes of the three pure groups from the three provinces (Hebei, Henan, and Shandong) of the two regions have genomic regions with different mosaic patterns derived from the two landrace groups. These findings may facilitate the development of wheat breeding strategies to target novel desired alleles in the future.

Keywords: bread wheat; SNP; population structure; genetic diversity; ancestry informative markers

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1. Introduction

Bread wheat (*Triticum aestivum* L.) is one of the most widely cultivated cereal crops in the world [1–3]. There has been increasing paleobotanical, archaeological, and genomic evidence revealing that wheat is an exotic crop to China that was probably expanded to China approximately 4500 years ago along the ancient Silk Road [2,4–8]. Since then, it gradually became one of the staple crops in China [9–11]. Bread wheat was likely introduced to northwest China first and then spread to east China and gradually to south and southwest China [12,13]. For thousands of years, numerous artificial selections have been carried out for the domestication of landraces to cultivated varieties, with the aim

to improve the yield and quality of grains and resistance to stresses [14–18]. After being introduced into China, bread wheat gradually differentiated into various ecotypes for adaptation to the different ecological environment in China.

It is necessary to study the population structure and genetic diversity of bread wheat in east Asia, particularly in China [3,19–21]. Since bread wheat was expanded into east Asia from its geographical origin, the southwestern coastal area of the Caspian Sea [1,6,22–27], it had little chance to hybridize with its tetraploid ancestors [10]. Some studies have indicated that Chinese wheat landraces and worldwide hexaploid wheat have similar differences in nucleotide diversity among the A, B, and D genomes [1,19,21]. Consistent with wild emmer wheat [28], genetically related bread wheat landraces have close geographical origins, and the population is generally distributed along certain geographical lines [10]. However, this phenomenon has rarely been reported in Chinese modern wheat breeding lines.

This study aims to explore the population structure and genetic diversity of a panel consisting of some Chinese modern wheat breeding lines mainly originating from the northern winter wheat region and the Huang-Huai River Valley's facultative wheat region. The panel was composed of 302 bread wheat accessions, which can reflect about 70 years of wheat breeding processes in some provinces of China, particularly in Hebei, Henan, and Shandong. The results may clarify whether genetically related Chinese modern wheat breeding lines have close geographical origins, and whether the genetic diversity decreases or increases along with the advancement of breeding. Finally, some landraces were used to explore the genomic regions contributing to differences in genomes among different geographical populations. During domestication, obtainment or loss of genetic variation of populations was associated with adaptability to adversity [29] and trait transformation such as grain yield, quality, and micronutrient content change [30]. Studying the population structure and genetic diversity is a foundation for the genetic mapping of a phenotype. Therefore, the findings are expected to facilitate the development of breeding strategies to target novel elite alleles of the desired phenotype in the future.

2. Materials and Methods

2.1. Study Regions

Due to differences in temperature, precipitation, and altitude across different geographical regions, wheat shows great differences in ecological adaptability in China. According to He et al. [31], China can be divided into ten agro-ecological regions for wheat: the northern winter wheat region, Huang-Huai River Valley's facultative wheat region, the middle and low Yangtze Valley autumn-sown spring wheat region, the southern autumn-sown spring wheat region, the southwestern autumn-sown spring wheat region, the northeastern spring wheat region, the northern spring wheat region, the northwestern spring wheat region, the Qinghai-Tibetan plateau spring-winter wheat region, and the Xinjiang winter-spring wheat region (Figure 1). Among them, the northern winter wheat region (NW; mainly including Hebei, Shanxi, Beijing, and Tianjin) and the Huang-Huai River Valley's facultative wheat region (HH; mainly including Henan, Shandong, Shaanxi, North Anhui, and Jiangsu) are the most important wheat-producing regions (Figure 1), totally accounting for 52% of the total harvested area and 60–70% of the total wheat production in China [31]. Therefore, it is necessary to study the population structure and genetic diversity of wheat varieties in these two regions.

2.2. Plant Materials

The studied panel was composed of 302 bread wheat accessions, comprising twelve landraces and 290 Chinese cultivars (lines) (Table S1). Most of the 290 accessions originated from NW and HH (Table S1), and these accessions covered fourteen provinces/municipalities of China, including Hebei (84), Henan (61), Shandong (59), Shanxi (19), Beijing (15), Jiangsu (13), Shaanxi (11), Hubei (8), Anhui (6), Sichuan (4), Gansu (3), Heilongjiang (2), Ningxia (3), and Tianjin (2) (Table S1). These accessions were approved from 1954 to 2021,

which therefore can reflect about 70 years of wheat breeding processes in northern China, particularly for NW and HH (Table S1).

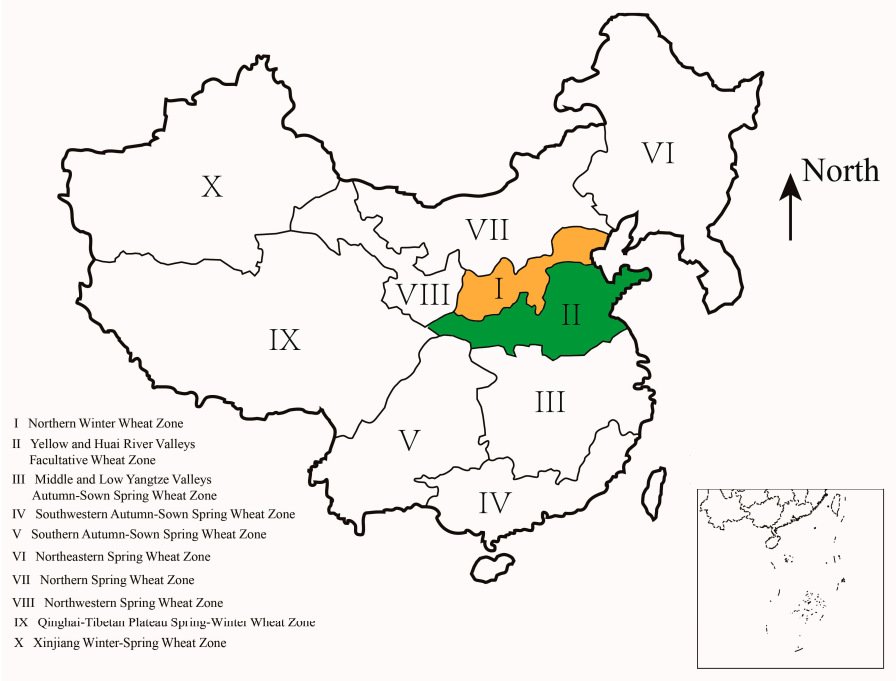

Figure 1. Division of wheat agro-ecological regions in China. The northern winter wheat region and the Huang-Huai River Valley's facultative wheat region are colored orange and green, respectively. The original map was drawn according to He et al. [31] using software Arcgis 10.2 and Adobe Illustrator CS6.

2.3. DNA Extraction and Genotyping by a Wheat 15K SNP Array

The genomic DNA of each bread wheat accession was extracted from the third fully unfolded leaf using the DNA quick Plant System by Tiangen Biotech (Beijing, China) Co., Ltd., (www.tiangen.com; accessed on 8 May 2022) according to the manufacturer's instructions. After extraction and dilution, the DNA at a concentration of 50 ng uL^{-1} was used for genotyping with a 15K SNP array from China Golden Marker Co., Ltd., (Beijing, China). After nucleic acid amplification, labeling, and chip hybridizing, the raw data were obtained. In order to obtain qualified genotype data of each sample, we conducted both sample and marker quality control according to the workflow presented in Figure S1. The SNPs with minor allele frequency (MAF) < 0.05 and missing data >20% were removed. After filtering, a ped file and a map file including 13,705 SNPs were obtained from the total 15,020 SNPs in the bread wheat panel, including 13,196 markers with known physical positions in the reference genome of Chinese Spring V1.0 [32] and 509 markers with unknown physical positions (Figure 2A). The 509 SNPs in unknown physical positions were reserved for subsequent analysis because they were just mapped to scaffolds but not in proper regions on the 21 chromosomes of Chinese Spring V1.0 when the reference genome was assembled.

2.4. Population Structure Analysis

A maximum likelihood tree was constructed for the 302 bread wheat accessions by using the software iqtree v.1.6.1.2 [33]. Briefly, the ped and map files were converted into a vcf file by using Plink version 1.90b6.18 [34], and the generated vcf file was converted into a fasta file by using the python script vcf2phylip.py (https://github.com/edgardomortiz/vcf2phylip/releases accessed on 10 May 2022). The fasta file was run by using iqtree v.1.6.1.2 with the parameter "-m MFP --alrt 1000 -b 1000". The generated maximum likelihood tree was visualized by using the online tool iTOL (http://itol.embl.de/ accessed on 15 July 2022).

Before inferring the genetic ancestry of each accession, Plink version 1.90b6.18 was used to convert the ped and map files into the structure_in format as the input file of STRUCTURE v.2.3.4 [35]. The software STRUCTURE v.2.3.4 was employed to infer the genetic ancestry of each accession with a predetermined number of clusters (K) from 2 to 7. Each K value was run 10 times with the main parameters provided in Supplementary Materials. The Markov chain in each analysis was set to 100,000 burn-in steps and 200,000 further steps were used for parameter value estimation. The online software STRUCTURE HARVESTER [36] and CLUMPP_Linux64.1.1.2 [37] were used to process the STRUCTURE output and evaluate the most probable K value by examining the delta K. Principal component analysis (PCA) was performed to evaluate the genetic relationship for accessions by using the software Plink version 1.90b6.18.

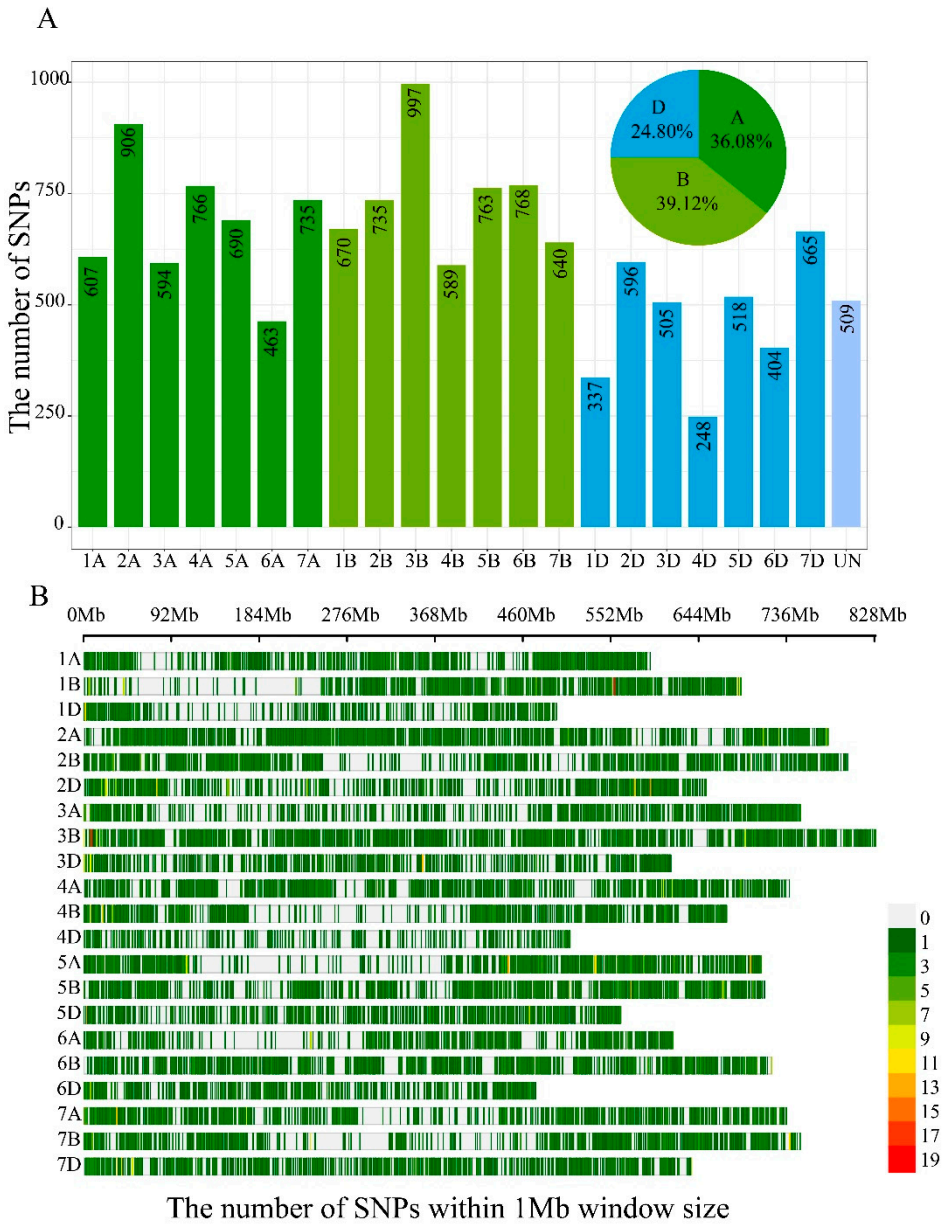

Figure 2. Distribution of 13,705 SNPs in the genome of wheat. (**A**) The number of SNPs for A, B, and D sub-genomes. (**B**) The number of SNPs within 1 Mb window size in the 21 chromosomes.

2.5. Genetic Diversity Evaluation

The fasta file with 13,705 SNP markers was divided into three fasta files according to the three geographical populations (NW, HH1, and HH2) (Table S1). We estimated the

nucleotide diversity (π) per base within populations with the software Dnasp5.0 [38] by using the corresponding fasta files as input files, respectively. The software Plink version 1.90b6.18 was employed to calculate the minor allele frequency (MAF) at each locus of each population by using the ped and map files as input files with the parameter "--freq --noweb --missing --withing pop.cov", where "pop.cov" is the grouped file of samples from the three geographical populations. At each population, the polymorphism information content (PIC) and the expected heterozygosity (H_{exp}) at each locus were calculated by using the following formulas reported by Zhou et al. [39]:

$$PIC = 1 - p^2 - q^2 - 2p^2q^2$$

$$H_{exp} = 1 - p^2 - q^2,$$

where p and q are the frequencies of the two alleles at a locus within the population according to Guo and Elston [40], respectively. After calculating PIC and H_{exp} at the 13,705 loci of each population, we averaged the PIC and H_{exp} as the population's PIC and H_{exp}, respectively.

2.6. Inference of Ancestry Informative Markers

The analysis was carried out in four steps. First, one gene pool for each of the five bread wheat groups (Hebei, Henan, Shandong, Landrace1, and Landrace2) was constructed based on the previously reported method [39,41,42]. Briefly, if a locus had two or more variants, the minority variants were treated as errors in a group. If variants in a locus had the same frequency, they were selected randomly. After the five gene pools were constructed, we selected those unique loci (i.e., loci with different genotypes in the two landrace groups) in group Landrace1 and Landrace2. Then, in the three pure cultivar groups, we traced their ancestry informative genotypes derived from the two landrace groups at each unique locus. Subsequently, SNPEFF was employed to annotate the shared SNPs between the landrace and cultivar groups [43]. The final results were visualized using the Circlize package (version 0.4.15) in R [44].

3. Results

3.1. Distribution of SNP Markers across the Wheat Genome

A total of 302 bread wheat accessions mainly from NW and HH were selected for genome-wide genotyping (Table S1). After genotyping and filtering, we obtained 13,705 high-quality SNPs across the 21 chromosomes (13,196) of wheat and the chromosome Unkown (chrUN) (509) (Figure 2A). The number of SNPs from chromosome 1A to 7A was 607, 906, 594, 766, 690, 463, and 735 (Figure 2A), respectively. In the B and D sub-genomes, we found 670, 735, 997, 589, 763, 768, and 640 SNPs from 1B to 7B, and 337, 596, 505, 248, 518, 404, and 665 SNPs from 1D to 7D, respectively (Figure 2A). The highest proportion (39.12%) of SNPs was mapped in the B sub-genome, followed by the A sub-genome (36.08%) and the D sub-genome (24.80%) (Figure 2A). Although SNPs were unevenly distributed among sub-genomes, they were evenly distributed on each chromosome (Figure 2B).

3.2. Phylogenetic Relationship in the Bread Wheat Panel

The 13,705 loci generated by genotyping were used for population genetic analysis. A phylogenetic tree and population structure are presented in Figure 3. Three major populations (A, B, and C) could be clearly observed from the phylogenetic tree. In addition, some accessions were located in some intermediate positions among the three major groups, which were considered admixture types (Figure 3A). Population structure analysis was performed to estimate the individual ancestry and admixture proportions of each accession when assuming the existence of certain populations. By using the simulating population number (K) from 2 to 7, K = 3 was found to be the closest to the real clustering state of the accessions for the appearance of the highest delta K value (Figure 3B). Moreover, the

302 bread wheat accessions were split into three groups, which was consistent with the results of the phylogenetic tree (Figure 3C). We assigned each accession to its corresponding population (A, B, and C) when its ancestral coefficient was greater than 0.5 at K = 3. The accessions with ancestral coefficients lower than 0.5 in each group were assigned to the admixture group. Then, the geographical distribution of accessions of each of the populations A, B, and C was examined, respectively. As a result, the distribution of accessions in the three populations was roughly in conformity with the three geographical origins, including NW (A, most samples from Hebei), HH1 (B, most samples from Henan-Shaanxi), and HH2 (C, most samples from Shandong) (Table S1).

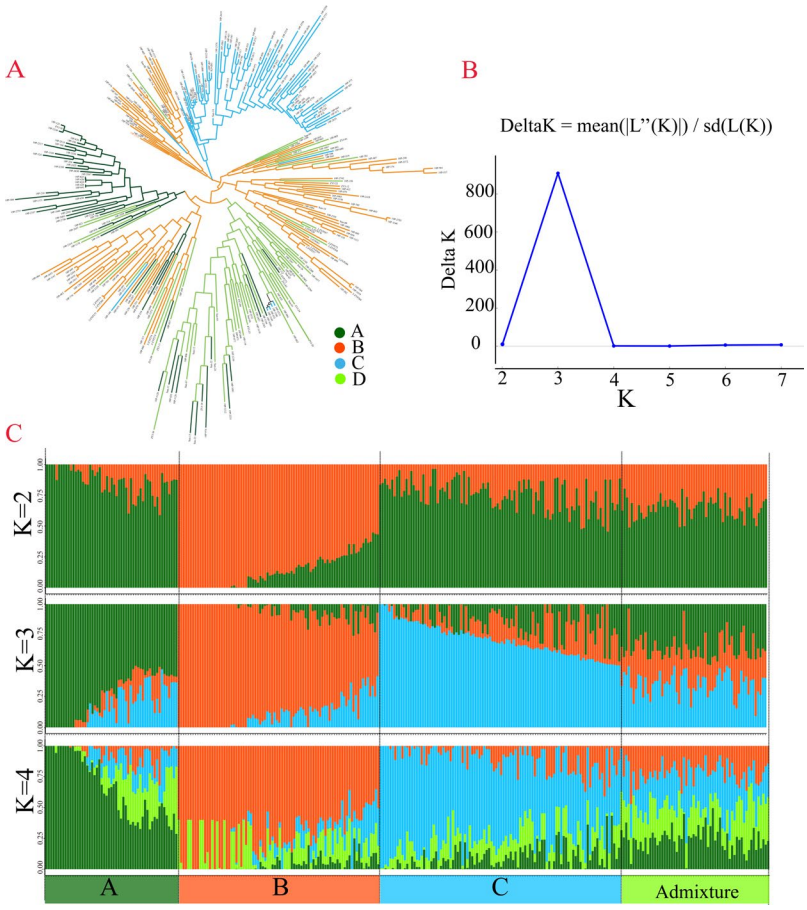

Figure 3. Phylogenetic tree and population structure of 302 bread wheat accessions. (**A**) The phylogenetic tree of the 302 bread wheat accessions. (**B**) The delta K values when K was 2 to 7. (**C**) The population structure plots of the 302 bread wheat accessions when K was 2 to 4.

According to the first and second eigenvectors of PCA, all accessions could be divided into three groups (Figure 4A), which were consistent with populations A, B, and C in the phylogenetic tree and population structure analysis results. Hence, this result further verified the phylogenetic relationships among the accessions obtained from the phylogenetic tree and population structure analysis (Figure 3A,C). Those accessions assigned to the admixture group in the phylogenetic tree (Figure 3A) and the population structure analysis (Figure 3C) were also found to be located in intermediate positions of the three groups (Figure 4A). Based on the 99% confidence intervals of the location of accessions, we found a lower genetic diversity for the C group than for the A and B groups (Figure 4A). When coloring all accessions according to their geographic distributions, we found that the A, B, and C groups were roughly represented by most studied accessions from NW (mainly derived from Heibei), HH1 (mainly derived from Henan-Shaanxi), and HH2 (mainly derived from Shandong), respectively (Figure 4B). These results suggested that modern wheat

breeding lines in northern China have obvious genetic differentiation due to environmental differences between or within agro-ecological regions.

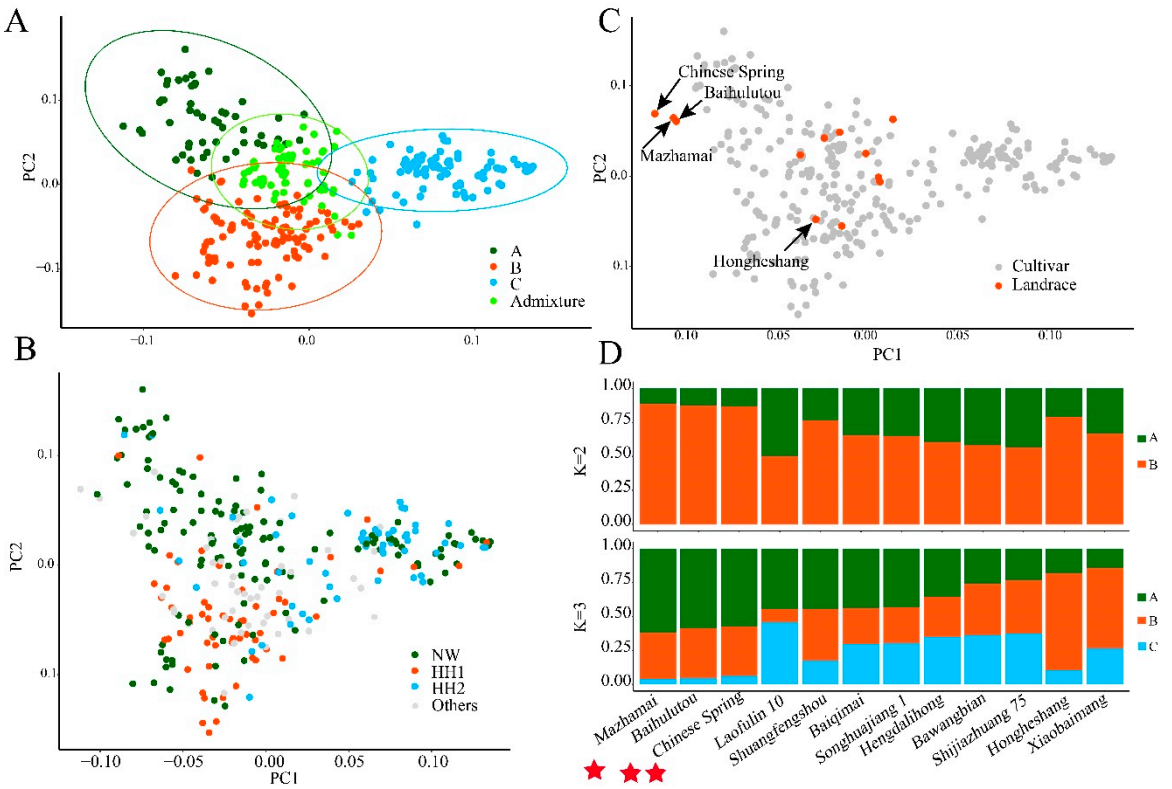

Figure 4. Principal component analysis (PCA) of 302 bread wheat accessions. The (**A**–**C**) panels show the same PCA colored according to different factors. (**A**) Positions of the four assigned groups (A, B, C, and Admixture) according to the results at K = 3 (Figure 3C). The small solid circles represent wheat accessions, and the large hollow circles represent the 99% confidence interval of the location of the accessions in the four groups. (**B**) All accessions were colored according to their geographic distributions. (**C**) Twelve landraces were colored in the PCA scatter plot. (**D**) Population structure of twelve landraces at K = 3. Three red pentagrams represent three materials that belong to the same category.

Obvious evolutionary divergence could be observed within the studied landraces in the PCA scatter plot when these accessions were colored (Figure 4C). Three landraces (Chinese Spring, Baihulutou, and Mazhamai) were separated from the other nine accessions (Figure 4C), and they had a higher ancestral coefficient of the NW group (Figure 4D). However, most of the landraces showed a mixed state (Figure 4D), i.e., the ancestral coefficients of NW, HH1, and HH2 were lower than 0.5. These results suggested that the landraces of bread wheat might have a higher genetic heterozygosity than the bred varieties.

3.3. Genetic Diversity within the Three Geographical Groups

Since the above population structure analysis and PCA results indicated that the ancestral components of these accessions are related to their geographical distribution (Figures 3C and 4B), it is necessary to separately evaluate the genetic diversity of accessions from NW, HH1, and HH2. Four indices (π, MAF, PIC, and Hexp) were used to evaluate the genetic diversity within the three groups. The results revealed that within the HH agro-ecological regions, HH1 had higher nucleotide diversity (π = 0.31167), minor allele frequency (MAF = 0.2663), polymorphism information content (PIC = 0.2668), and expected heterozygosity (H_{exp} = 0.3346) than HH2 (Table 1). NW had very close genetic diversity indices to HH1 with π = 0.31058, MAF = 0.2597, PIC = 0.2675 and Hexp = 0.3360.

Table 1. Estimate of genetic diversity per base pair for three groups.

Groups	n	π	MAF	PIC	Hexp
Region:					
HH1	72	0.31167	0.2663	0.2668	0.3346
NW	120	0.31058	0.2597	0.2675	0.3360
HH2	59	0.27835	0.2353	0.2378	0.2940
Years:					
Before 2000	39	0.34995	0.2834	0.2728	0.3435
2000–2009	98	0.33023	0.2647	0.2747	0.3458
After 2009	155	0.28510	0.2489	0.2629	0.3291

Note: n: number of accessions; π, nucleotide diversity; MAF, minor allele frequency; PIC, polymorphism information content; Hexp, expected heterozygosity.

Moreover, according to their breeding years, the 292 bread wheat cultivars were divided into three groups: before 2000, 2000–2009, and after 2009. The four genetic diversity indices (π, MAF, PIC, and H_{exp}) were also calculated within the three groups, respectively. Although the number of samples varied greatly among different groups, it could be clearly observed that the group with breeding years closer to the present had lower genetic diversity as indicated by the lower π and MAF values (Table 1).

3.4. Genomes of the Three Geographical Groups Showed Differently Patterned Mosaics of Different Landrace Groups

The population structure analysis results indicated that the optimal population number K was 3, and the three groups were related to three geographical origins (NW, HH1, and HH2) (Figures 3C and 4B; Table S1). Furthermore, PCA could divide the landrace accessions into two groups: Landrace1 (including Mazhamai, Baihulutou, and Chinese Spring) and Landrace2 (including Laofulin 10, Shuangfengshou, Baiqimai, Songhuajiang 1, Hengdalihong, Bawangbian, Shijiazhuang 75, Hongheshang, and Xiaobaimang) (Figure 4C). Hence, it would be interesting to determine which genomic regions of the three geographical groups can be traced back to the two landrace groups. Based on the results of K = 3 in the population structure inference, we selected individuals that originated from Hebei (representing the NW group), Henan (representing the HH1 group), and Shandong (representing the HH2 group) with ≥80% corresponding ancestry coefficients to be added into the pure Hebei, Henan, and Shandong groups, respectively. In total, 55 accessions met the selection criteria (Table 2). We selected the ancestry-informative marker inference method to infer the genetic effect of landraces on cultivars by constructing gene pools for the five bread wheat groups (three geographical groups and two landrace groups) based on major allele frequency differentials in each locus (Figure 5). The following analysis would be focused on the 13,705 SNP loci. As a result, in 21 chromosomes, the majority of the loci of the Landrace1 group had higher major allele frequencies than those in the Landrace2 group, suggesting that the Landrace1 group was more homogeneous while the Landrace2 group was more heterozygous (Figure 5a–c). In 13,705 loci, we found 6057 loci showing different genotypes in two landrace groups, suggesting possibly great genetic differentiation between the two landrace populations. In addition, among these 6057 loci, 2353 loci shared the same genotypes between the Landrace1 group and the pure Hebei group, while only 1720 or 1423 loci shared the same genotype between the Landrace1 group and the pure Henan group or the pure Shandong group (Table 3). In addition, the Landrace2 group shared more loci of the same genotype with the pure Henan (4337) and Shandong (4634) groups but fewer loci with the pure Hebei group (3704) (Table 3). These results indicated that the Landrace1 group might have a higher genetic connection to Hebei bread wheat, while the Landrace2 group might have greater impacts on the genomic composition of bread wheat from Henan and Shandong. Furthermore, in these loci shared between the landrace and cultivar groups, 48, 63, 36, 75, 37, and 74 loci were annotated as missense variants in Landrace1-Hebei, Landrace2-Hebei, Landrace1-Henan, Landrace2-Henan, Landrace1-Shandong, and Landrace2-Shandong, respectively.

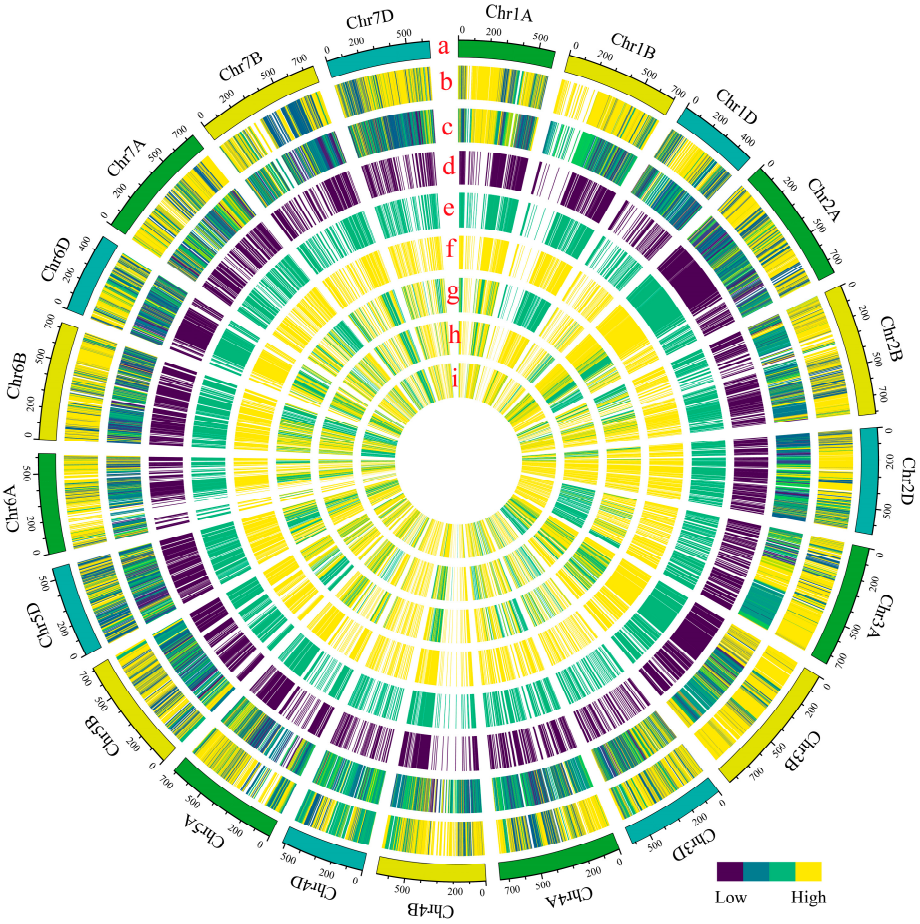

Figure 5. Graphical genotypes of ancestry informative markers in the three geographical groups. The circos plot was composed of nine circles (**a**–**i**). (**a**) Genome coordinates of 21 chromosomes. (**b**) Major allele frequencies of the Landrace1 group (including landrace accessions Chinese Spring, Baihulutou, and Mazhamai). (**c**) Major allele frequencies of the Landrace2 group (including landrace accessions Laofulin 10, Shuangfengshou, Baiqimai, Songhuajiang 1, Hengdalihong, Bawangbian, Shijiazhuang 75, Hongheshang, and Xiaobaimang). (**d**) A total of 5844 loci with different genotypes for the two gene pools of the landrace groups. (**e**,**f**) Genotypes of the Landrace1 group (**e**) and Landrace2 group (**f**) in the 5844 loci were colored green and yellow, respectively. (**g**,**i**) In the 5844 loci, genotypes of the pure Hebei group (**g**), the pure Henan group (**h**), and the pure Shandong group (**i**) were colored according to the genotypes of the Landrace1 group and the Landrace2 group.

Out of 6057 loci, 5844 loci on 21 chromosomes were used to detect which genomic region of the three geographical groups can be traced back to the two landrace groups. As a result, genomes of the three geographical groups showed differently patterned mosaics coming from the two landrace groups (Figure 5e–i). For example, the Landrace1 group contributed more loci with the same genotype to the pure Hebei group in chromosomes 1B, 3B, 5B, 5D, and 7A (Figure 5h), while Landrace2 group contributed more loci with the same genotype to the pure Henan group in chromosomes 1B, 2D, 4D, and 5D (Figure 5h) and the pure Shandong group in chromosomes 1A and 3A (Figure 5i). These results also indicated that the two landrace groups had inconsistent contribution to the distribution of genome on 21 chromosomes in the three geographical populations.

Table 2. List of the 67 wheat accessions for inference of ancestry informative markers.

Code	Accessions Name	Group	Code	Accessions Name	Group
1	Chinese Spring	Landrace1	35	Yingman 208	Shandong
2	Baihulutou	Landrace1	36	Shannong k32561	Shandong
3	Mazhamai	Landrace1	37	Shannong 27	Shandong
4	Laofulin 10	Landrace2	38	Taishan 5366	Shandong
5	Shuangfengshou	Landrace2	39	Shannong 2149	Shandong
6	Baiqimai	Landrace2	40	Lumai 14	Shandong
7	Songhuajiang 1	Landrace2	41	Daimai 2251	Shandong
8	Hengdalihong	Landrace2	42	Jimai 60	Shandong
9	Bawangbian	Landrace2	43	Keyuan 026	Shandong
10	Shijiazhuang 75	Landrace2	44	Luyan 213	Shandong
11	Hongheshang	Landrace2	45	Yimai 1	Shandong
12	Xiaobaimang	Landrace2	46	Zimai 28	Shandong
13	Nongda 399	Hebei	47	Yimai 2	Shandong
14	Jifeng 717	Hebei	48	Yangguang 503	Shandong
15	Jinhe 9123	Hebei	49	Yangguang 10	Shandong
16	Shimai 22	Hebei	50	Yannong 836	Shandong
17	Jimai 817	Hebei	51	Jingyang 670	Shandong
18	Jimai 26	Hebei	52	Wennong 5	Shandong
19	Shimai 28	Hebei	53	Aikang 58	Henan
20	ShiH09-7075	Hebei	54	Zhoumai 35	Henan
21	Shi 4185	Hebei	55	Zhengyumai 9989	Henan
22	Shimai 12	Hebei	56	Cunmai 8	Henan
23	Shimai 14	Hebei	57	Dunfeng 801	Henan
24	Heng 11-6021	Hebei	58	Xinmai 28	Henan
25	Jimai 161	Hebei	59	Zhengmai 9023	Henan
26	Kenong 1006	Hebei	60	Yimai 6	Henan
27	Jimai 120	Hebei	61	Zhoumai 16	Henan
28	Kenong 8162	Hebei	62	Xun 2016	Henan
29	Kenong 1002	Hebei	63	Fengyuan 2017	Henan
30	Qingnong 9	Shandong	64	Xianmai 10	Henan
31	Qingmai 6	Shandong	65	Cunmai 12	Henan
32	Liangxing 99	Shandong	66	Fengdecunmai 10	Henan
33	Jimai 22	Shandong	67	Zhoumai 18	Henan
34	Shannong 24	Shandong			

Table 3. Number of SNPs sharing the same genotype between three geographic populations and two landrace groups.

Groups	Heibei	Henan	Shandong
Landrace1	2353	1720	1423
Landrace2	3704	4337	4634

4. Discussion

4.1. Genetically Related Chinese Modern Wheat Breeding Lines Have Close Geographical Origins

Domesticated crops will be confronted with acute adaptive challenges when transferred from their domestication centers to new latitudes [45]. Wheat has spread to a wide range of climates, where the environment can affect genetic selection to result in genetic variations [18]. Based on both population structure analysis and PCA, our population genetics analysis results demonstrated that most genetically related Chinese wheat modern breeding lines tend to have close geographical origins (Figures 3C and 4B), which is similar to the findings in a previous study of bread wheat landraces [8,10]. This phenomenon may be a result of the difference in the adaptability of bread wheat to different latitudes, temperature, and precipitation. However, the PCA scatter plot (Figure 4B) shows that some wheat accessions from the three populations (NW, HH1, and HH2) did not show great genetic distance from each other and even exhibited highly similar genetic components.

One possible explanation is that these three regions are geographically close with a narrow span of latitude, and it is relatively easy to improve the yield performance through the introduction and hybridization of cross-regional wheat varieties. This will lead to similar genetic components in some accessions from different regions. Actually, a previous study has indicated that the genetic distance of wheat landraces between the Tibetan plateau and northwestern China is not very great, possibly because the two zones are geographically close [10].

Environmental factors, including altitude, frost-free days, annual sunlight, temperature, precipitation, and soil type, may have driven the regional/local genetic divergence and altered the genetic diversity of landrace wheat, wild emmer wheat, and wild barley [10,39,46,47]. Artificial selection has been confirmed to be a major force shaping the population structure of wheat germplasm [3,14,48,49]. In modern wheat breeding lines, the genetic architecture of agronomic traits is shaped by the interaction between long-term artificial directional selection and early population genetic structure [50,51]. Studying the population structure and genetic diversity is critical for the genetic mapping of traits such as grain yield, quality, and micronutrient content [30]. A hypothesis was proposed that compared with the A and B sub-genomes, only a small *Aegilops tauschii* population genetically contributed the D sub-genome of hexaploid wheat, thereby causing lower nucleotide diversity and divergence frequency in the D sub-genome [1,6,10,27]. Besides the initial population size, artificial selection can also greatly shape the genetic diversity of the population. Our results clearly demonstrated that the genetic diversity (π and MAF) decreases with the advancement of wheat breeding (Table 1), possibly because during the breeding process, the effective population size of the parents is declining, and breeders only focus on a few traits for directed selection. However, the very small intervals in the groups '2000–2009' and 'after 2009' might cause a bias in the genetic diversity assessment of the two groups because many parents of varieties within the groups might be closely related to each other. The decline of genetic diversity often results in the deletion of genes for some key traits in modern breeding lines. Therefore, it is necessary to integrate some landraces and early breeding lines carrying excellent traits for the breeding of modern wheat lines in the future [52].

4.2. Modern Wheat Breeding Lines Have Mosaic Genomic Regions Derived from Different Landrace Groups

Although very few landraces are used as parents for hybridization in modern wheat breeding programs due to their undesirable plant height and yield, it does not mean that landraces have no genetic contribution to modern breeding lines. At present, research on the population genomics of wheat landraces has been mainly focused on genetic differentiation with modern breeding lines and searching for artificially selected genomic regions [2,10,14,53,54]. For instance, a study has indicated that about 6.7% of the wheat genome falls within the selective sweeps between landraces and cultivars [55]. The allelic erosion and a diversity bottleneck can be inferred through comparative genomics between landraces and modern breeding lines [2]. Just like the findings in maize and soybean [56,57], some artificially selected genomic regions contain the functional genes or loci that regulate known phenotypes for disease resistance, vernalization, quality, adaptability, and yield-related traits [2,55,58]. However, there have been few reports about the genomic relation between landraces and modern breeding lines.

According to the inference of ancestry informative markers, 2353 out of the 6057 loci shared the same genotypes in the Landrace1 group and the pure Hebei group, while only 1720 and 1423 loci shared the same genotype between the Landrace1 group and the pure Henan group and between the Landrace1 group and the pure Shandong group, respectively (Table 3). These results suggest that the Landrace1 group contributes more to the genetic composition of modern breeding lines from Hebei province. The Landrace2 group shared more loci with the same genotype with the pure Henan (4337) and Shandong (4634) groups but fewer loci with the pure Hebei group (3704) (Table 3), indicating that the Landrace2

group contributes more to the genetic composition of modern breeding lines from Henan and Shandong. Those missenses which were stop gained and stop retained variants shared by landrace-cultivar groups might show evolutionary benefits in the process of wheat domestication, while other variants such as intergenic region SNPs might result from the rearrangement of repetitive elements (Table S2). Furthermore, genomes of the three geographical groups showed differently patterned mosaics of the genomes derived from the two landrace groups (Figure 5e–i). In barley, Dai et al. [42] indicated that wild barley of the Fertile Crescent contributes more genomic regions to the genome of cultivated barley in chromosomes 1H, 2H, and 3H, while wild barley of Tibet contributes more genomic regions in chromosomes 4H, 5H, 6H, and 7H. In addition, Zhou et al. [39] reported that wild barley of Tibet genetically contributes more to cultivated barley of China than wild barley from the Fertile Crescent. Wheat landraces are highly valuable genetic and breeding resources. A better understanding of their relationship with modern breeding lines can help develop strategies to target novel elite alleles for future wheat breeding [2].

4.3. Conclusions and Prospects

Northern winter wheat region (NW) and the Huang-Huai River Valley's facultative wheat region (HH) are the most important wheat producing regions in China. Here, population genetic analysis of 302 bread wheat accessions revealed three main groups that are largely associated with geographical regions, including NW (mainly Hebei), HH1 (Henan-Shaanxi), and HH2 (Shandong). Genetic diversity decreases with the advancement of wheat breeding. Inference of ancestry informative markers indicated that modern wheat breeding lines exhibit mosaic genomic regions derived from different landrace groups. These findings deepen our understanding of the genomic changes driven by both human and ecological factors during domestication and may facilitate the development of breeding strategies to target novel elite alleles in the future.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy13092408/s1, Figure S1: A workflow for filtering raw data of the 15K SNP array; Table S1: List of 302 wheat accessions of the panel; Table S2: Summary of the annotated SNPs of the landrace-cultivar groups that share common genotypes.

Author Contributions: Y.Z. (Yingjun Zhang), X.R. and Y.P. designed the experiment. X.J., H.G., Q.L., G.W., Z.S., Y.Z. (Yun Zhao) and X.Z. did most of the experiments. X.J., H.G., Y.Z. (Yu Zhou), and W.H. conducted the data analysis. X.J. and H.G. drafted the manuscript. Y.Z. (Yingjun Zhang), X.R. and Y.P. revised the manuscript. All authors have read and agreed to the published version of the manuscript.

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